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Bamboo overabundance alters forest structure and dynamics in the Atlantic Forest hotspot

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ABSTRACT

With fast growth rates and clonal reproduction, bamboos can rapidly invade forest areas, drastically changing their original structure. In the Brazilian Atlantic Forest, where recent mapping efforts have shown that woody bamboos dominate large areas, the present study assessed the differences in soil and vegetation between plots dominated (>90% of bamboo coverage) and not dominated (<10% of coverage) by the native *Guadua tagoara*. Surface soil was physically and chemically analyzed, and trees at three size classes (seedling, sapling, and adult) were counted, identified and measured. New inventories were conducted to assess recruitment, mortality, and damage rates. Bamboo plots had more fertile soils (higher bases saturation and lower potential acidity) due to the preferential occurrence of *G. tagoara* on more clayey soils. Bamboo-dominated plots had lower density of adult trees (diameter >5 cm) and lower species density. In addition, overall tree diameter distribution was very different between environments, with bamboo plots having greater concentration of small-sized trees. Such differences are probably related to the general tendency of higher mortality, recruitment, and damage rates in bamboo plots. Greater physical (wind and bamboo-induced damages) and physiological stress (heat and light) in bamboo plots are probable causes of bamboo-dominated plots being more dynamic. Finally, we discuss the differences between Atlantic and Amazonian *Guadua*-dominated forests, causes, and possible consequences of bamboo overabundance to the Atlantic Forest conservation.

1. Introduction

Records of biological invasions are widespread in the ecological literature. Classic examples come from alien species that are introduced by man into a new environment (e.g. Vitousek et al., 1987) where they become dominant for different reasons (e.g. lack of predators or competitors). The consequences vary from the addition of new species to drastic disruptions on the community structure (Simberloff and von Holle, 1999; Mack et al., 2000). Nevertheless, there are records of native species becoming increasingly dominant in its original range, a phenomenon known as overabundance (Garrot et al., 1993). Generally, overabundant species are opportunists that respond positively to changes in the original community, a common feature of human-modified landscapes. Traditionally seen as a phenomenon that needs control, biological invasions by exotic species are one of the most conspicuous impacts in natural ecosystems, and its study has provided some important ecological and evolutionary insights (Rejmánek, 1996; Sax et al., 2007). Although regarded as a phenomenon with similar impacts (Garrot et al., 1993), the effects of overabundant native species are less known.

Many woody bamboos (Poaceae: Bambuseae) are typical examples of invasive plants, having many attributes of successful invaders. The production of large amounts of small seeds and small periods of dormancy promote efficient colonization of new sites (Rejmánek and Richardson, 1996; Williamson and Fitter, 1996; Veldman and Putz, 2011), especially disturbed ones (Burman and Filgueiras, 1993). Once established, fast growth and clonal reproduction (sometimes including reiterative growth) increase bamboos' ability to compete for space, and to form dense stands (Silveira, 2005). Its reproduction and growth strategies work together to sustain the occupancy for long periods of time (Young, 1991; Griscom and Ashton, 2006). Since woody bamboos are essentially forest species (Clark, 1997; Judziewicz et al., 1999), bamboo-dominated areas usually play an important part on the structure and dynamics of forest ecosystems (Veblen, 1982;

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Okutomi et al., 1996). In this sense, there is a general agreement that bamboos compete with other species, reducing woody species density and diversity (Taylor and Zisheng, 1988; Silveira, 2005) and sometimes bringing forest succession to a standstill (Griscom and Ashton, 2006). Bamboos also affect seed dispersal patterns, influencing forest regeneration on its early stages (Rother et al., 2009). Forest soils and nutrient cycling are also affected by high bamboo dominance that may have soils and litter poorer in some nutrients (Veblen, 1982; Tripathi et al., 2006).

Unconstrained bamboo expansion can lead to the formation of the so-called bamboo forests, well-known in Eastern Asia (Taylor and Zisheng, 1988; Okutomi et al., 1996). In South America, there are vast areas in southwestern Amazon dominated by native *Guadua* species (>160,000 km^2), where density varies from 1.900 to 3.800 culms ha^{-1} (Griscom and Ashton, 2006; Nelson et al., 2006). More recently, attention was directed to southeastern Brazil where mapping efforts revealed that considerable parts of the remaining Atlantic Forest are dominated by woody bamboos. In southern São Paulo State, for instance, there is evidence that one third of the forest remnants may be dominated by woody bamboos, mainly *Guadua tagoara* (Fantini and Guries, 2007; Araujo, 2008). Other important remnants in Rio de Janeiro state (i.e. Itatiaia, Bocaina, and Serra dos Orgãos National Parks) also present areas dominated by this species (R.A.F. Lima, pers. observation). Although *G. tagoara* is native, the situation is somewhat alarming since there is evidence of bamboo expansion (Alves, 2007). After analyzing aerial photographs between 1962 and 2000 in a 40,000-ha protected area, Araujo (2008) reported an increase of ca. 2000 ha in the forest class enclosing bamboo-dominated forests. Thus, in the highly threatened Atlantic Forest (Ribeiro et al., 2009), conservationists currently see the overabundance of *G. tagoara* and other woody bamboos as major threats (Araujo, 2008).

However, the origin of *G. tagoara* overabundance is still unclear. Some have argued that it is induced by human activities, such as crops, timber, and/or palm-heart extraction (Fantini and Guries, 2007; Araujo, 2008). But natural disturbances or specific types of soil may also create suitable environments to bamboo colonization (Griscom and Ashton, 2006; Nelson et al., 2006). Independently of their origin, the overabundance of bamboos in the Atlantic Forest is an issue that deserves close attention. Obviously, any intervention should be preceded by the understanding of the expansion processes and consequences. Similarly to southwestern Amazon (Nelson et al., 2006; Griscom and Ashton, 2003), forests dominated by *G. tagoara* have lower densities of adult trees (Fantini and Guries, 2007). Despite of the effects of *G. tagoara* on forest structure, studies on the underlying processes that generate such differences are largely missing. In addition, we still do not know what the influences of *G. tagoara* overabundance are on species density and soil nutrient availability.

This study was conducted in São Paulo state, where woody bamboos have become a real issue for biodiversity conservation. The aim was to understand the effects of *G. tagoara* overabundance on different environmental features. More specifically, we assessed how *G. tagoara* affects soil physical–chemical properties, forest structure and tree species diversity by comparing bamboo-free and bamboo-dominated areas within a 10.24-ha plot. We evaluated if differences on forest structure between environments were accompanied by different dynamics, in terms of recruitment and mortality. In addition, we assessed Griscom and Ashton's (2006) hypothesis that bamboo-induced damages are the main causes of the self-perpetuating cycle in *Guadua*-dominated forests. Finally, we discuss the origin of bamboo overabundance, and its influence in the Atlantic Forest conservation.

2. Material and methods

2.1. Study site

The study site is the Carlos Botelho State Park (PECB) which covers 37 644 ha of the Atlantic Forest of southern São Paulo State, Brazil, one of the largest and well-conserved Atlantic Forest continuums. Data collection was carried out in 10.24-ha (320 × 320 m) permanent plot established in 2002 in the Sete Barras county (plot coordinates: 24°10′S and 47°56′W) subdivided into 20 × 20-m subplots. Local climate is classified as humid subtropical with no dry season (Cfa) with mean annual temperature and precipitation of 22 °C and 1584 mm, respectively. Although there is no dry season, rainfall gets below 50 mm from April through September, especially during El-Niño years. The plot was placed at steep slopes with altitudes varying from 350 to 450 m a.s.l. Plot soils developed over granites and colluvionar deposits, and were classified as Haplic Cambisols (Inceptisols) and Fluvisols/Leptosols (Fluvents/Udorthents; Rodrigues, 2005). Plot vegetation is an old-growth Lower Montane Rain Forest, with an average canopy height of 20 m. Palms and tree ferns are abundant, while Marantaceae and Araceae are common in the herb stratum. Families rich in tree species inside the plot are Myrtaceae, Fabaceae, Rubiaceae, Lauraceae, and Sapotaceae. Although there is no recent record of large human impacts, disturbances related to the illegal extraction of palm-heart (*Euterpe edulis*) are common.

2.2. Bamboo species

Almost one third of the 10.24-ha plot is covered by large areas (mainly >1000 m^2) with great dominance of woody bamboos, regionally known as *taquaral* (see online Supplementary material), where the great density of culms makes it hard to walk through. The canopy is markedly lower and discontinuous, enhancing light entrance (Lima and Gandolfi, 2009). In the studied plot, the *taquarais* are formed solely by *G. tagoara* (Nees) Kunth, a large-sized, semi-scandent woody bamboo. Culms are green, hollow (often filled with water), and scandent towards the top, with heights and girths of 8–15(−20) m and 5–10 cm, respectively (Londoño, 2001). They grow fast upwards (up to 20 cm day^{-1} – Alves, 2007) and then bend over the surrounding vegetation, aided by their sharp recurved thorns. Description of *G. tagoara* showed that the species has long-necked, pachymorph rhizomes that allow combined running and clumping growth strategies (Alves, 2007). The species is monocarpic (lifespan is probably 10–25 yr) with locally synchronized, mast-flowering spread over three or more years (Alves, 2007). The massive amounts of seeds promptly form dense seedling banks below and around senescent clumps (around 300 seedlings m^{-2}). *G. tagoara* is endemic to the Atlantic Lower Montane and Montane Rain Forests of Brazil, ranging from Bahia to Santa Catarina States (Londoño and Clark, 2002). Morphology and growth strategies are similar to the Amazonian *Guadua weberbaueri* and *Guadua sarcocarpa* (Silveira, 2005; Griscom and Ashton, 2006).

2.3. Study design

The 10.24-ha plot was completely surveyed in January 2006 and all areas dominated by *G. tagoara* were delimited. The resulting map was used to classify the 20 × 20-m plots into two groups: bamboo plots, i.e., plots containing ⩾90% of its area covered by *G. tagoara*-dominated stands; and non-bamboo plots, i.e., plots containing <10% of bamboo-dominated stands. This last group includes the other types of canopy conditions of the plot, namely closed-canopy and canopy gaps not dominated by bamboos. To minimize possible noises related to unknown bamboo-dominance in plots bordering bamboo-dominated areas, plots with >10 and <90% of bamboo coverage were not considered here. In order to keep the proportion of the two environments during plot selection (one third of the 10.24-ha plot is bamboo-dominated areas), non-bamboo plots were randomly selected until their number were approximately twice the number of bamboo plots (i.e. 49 bamboo vs. 107 non-bamboo plots). Because a parallel study involved floristic data comparison between environments, this proportion of bamboo vs. non-bamboo plots was also kept during sapling sampling (details in Section 2.4). Besides bamboo dominance, predominant topographic position (i.e. hilltop, slope and valley-bottom) and soil type were noted for each plot. Since the 10.24-ha plot corners were georeferenced, the coordinates at the center of each plot were also obtained.

2.4. Sampling methods

Soil samples were taken at the center of all 20 × 20-m plots at two different depths: 0–5, and 5–20 cm. Each soil sample was analyzed for texture and nutrients using standard procedures (EMBRAPA, 1997) to obtain pH (in water suspension), organic matter, phosphorus (P), sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), aluminum (Al^{3+}), potential acidity (Al + H), and soil fraction of sand, silt and clay. From these variables, the sum of exchangeable bases (SEB), cation exchange capacity (CEC), base saturation, and aluminum saturation were obtained.

Vegetation sampling focused on woody species and palms (tree ferns and lianas were excluded) divided into three size classes, which are referred here as seedlings (individuals up to 30 cm tall), saplings (above 1 m tall and below 4.8 cm of stem diameter at breast height – dbh) and adults (dbh $\geqslant$ 4.8 cm). Size classes were sampled using 20 × 20 (adults), 10 × 10 (saplings), and 1 × 1-m (seedlings) nested plots. The 20 × 20-m plots wherein the smaller nested plots were established were randomly chosen among the selected 20 × 20-m plots (see Section 2.3). The position of the nested plots inside the 20 × 20-m plot was also chosen at random, although some adjustments were made to guarantee that all plots were entirely inside bamboo or non-bamboo sites. Inside all plots, individuals were tagged, counted and identified to species level. Stem diameter measures were carried out at ground and breast height (1.3 m) for saplings and at breast height for adults in order to assess tree diameter distribution. No diameter measurements were taken for seedlings. For saplings and trees, diameter measures included stem ramifications below breast height for individual basal area determination. Exclusively for saplings, the presence of resprouts from past stem breakage and the status of each individual (erect, bent or horizontal) were also noted. Botanical specimens were collected whenever necessary and vouchers are found at the ESALQ/USP herbarium (ESA).

New censuses were carried out to assess recruitment and mortality for each size class. Census intervals correspond to the periods between May–October 2002 and August–January 2005 (~2.5 yr) for adults, and June–July 2005 and June–July 2006 for saplings (1 yr). Seedlings were sampled in two different periods: July 2004–June 2005 and January–December 2008 (1 yr each). For this size class, mortality was evaluated monthly (11 censuses intervals) and recruitment was evaluated bimonthly (five intervals). Since some 10 × 10-m plots were established in 2006, mortality and recruitment information are not available for all sapling plots. For saplings, besides recruitment and mortality, information on new damages was also noted. A new damage was considered as any stem/crown injury not previously recorded in the first inventory and/or changes in stem positioning clearly related to a falling branch, trunk or bamboo culm. The determination of causes of death was made only for saplings (field determination of causes of death was quite difficult for seedlings and adults for different reasons). Individual death was only considered when there was no evidence of life, such as resprouts or any living parts; otherwise, the individual was classified as damaged. Because of illegal *Euterpe edulis* harvesting, deaths and damages directly or indirectly related to this activity were not considered. *E. edulis* illegally harvested were kept in the database and had their diameter estimated (see Supplementary material for details).

2.5. Data analysis

Soil and vegetation variables were treated to obtain a single value for each plot. Since the general soil tendencies were the same at both depths, results from samples at 0–5 and 5–20 cm depths were averaged for each plot. For tree density, basal area and species density analysis, data used for saplings and adults correspond to living individuals at the last census. For seedlings, we averaged measurements of density, richness, mortality, and recruitment of all census intervals. Basal area was estimated as the sum of the cross-sectional area of all stems. Number of deaths and recruits were used to obtain the annual mortality (m) and recruitment (k) per plot using the following equations (Sheil and May, 1996):

$$m = 1 - (N_t/N_o)^{1/t} \tag{1}$$

$$k = \lambda \exp(\lambda t) N_r / (\exp(\lambda t) - 1)A \tag{2}$$

where N_t, N_o, and N_r are the number of individuals at time t (census interval in yr), the initial number of individual and the number of recruits, respectively; λ is the exponential mortality coefficient ($\lambda = -\ln(1 - m)$; Sheil et al., 1995); and A is the plot area (in m^2; Eq. (2) was rearranged to express k as a function of N_r and λ). In this equation, λ refers to the overall mean of λ for each size class. The inclusion of this last term provides the unbiased estimate of recruitment, since it accounts for recruits that died between consecutive censuses (Sheil and May, 1996). Sapling damage was calculated using Eq. (1), where N_t was replaced by the number of undamaged individuals at time t.

All variables (except diameter distribution) were analyzed using a general framework based on linear or generalized linear regression models (Pinheiro and Bates, 2000; Zuur et al., 2009), were the type of forest (i.e. bamboo and non-bamboo) was treated as categorical variable. First, data was inspected to select the best error distribution (e.g. gaussian, poisson, negative binomial) and to test for the presence of heteroscedasticity and/or spatial autocorrelation. Then models were constructed and validated using the following approach (Zuur et al., 2009). After determining the model random-structure, the optimal fixed-structure was determined by removing variables from the over-parameterized model until only significant ones were present. Finally, the optimum model was inspected for significant effects of bamboo-dominance using a standard t-test applied to the regression parameters. Exceptions to this approach were variables with excessive number of zeros (e.g. adult mortality) or when the addition of random effects proved to be unnecessary. Two-part models were used to deal with the excess of zeros, while generalized least squares were used in the last case. Since the number of species depends on the number of individuals in a non-linear fashion, plot abundance was always added as a covariate to model species density using a non-linear link function (nonlinear generalized least squares). A summary of the models structure is provided in the Supplementary material.

To compare diameter distributions, a single dataset was created by putting together data from all plots for each forest type (saplings <1.3 m tall were assigned as having dbh close to zero for analytical convenience). For multi-stemmed individuals, only the dbh of the largest stem was used. Since saplings and adults were sampled using different plot sizes (10 × 10 and 20 × 20-m), sapling abundance was corrected by the ratio of sapling to adult plot size. We fitted the Gamma probability density function (PDF) to the dbh distribution of each type of forest using maximum likelihood techniques and then compared the fits based on their parameter estimates (Burnham and Anderson, 2002; Bolker, 2008). The Gamma outperformed other commonly used PDFs, such as Weibull, lognormal and negative exponential (results not shown). The same procedure was used to compare adult ($\geqslant$4.8-cm dbh) distribution, although we used the Gamma truncated at 4.8. During all analysis (soil, vegetation, and diameter distribution), model selection was based on the Akaike Information Criterion for small samples (AIC_c) or on model residual deviance, whenever the AIC_c was not available. Differences in AIC_c values (i.e. ΔAIC_c) higher than log(8) were regarded as indicators of different fits between two models (Burnham and Anderson, 2002). All analyses were performed in R (www.R-project.org), using MASS (Venables and Ripley, 2002), nlme (Pinheiro et al., 2008), pscl (Zeileis et al., 2008; Jackman, 2010), and bbmle (Bolker, 2009). The basic R codes are available upon request from the authors.

3. Results

3.1. Soil properties

Overall, the surface soil was sandy clay loam, strongly acid (pH = 3.96 ± 0.27), and highly distrophic (base saturation = 17.2 ± 8.2%), although relatively rich in organic matter (OM = 40.8 ± 9.0 g dm^{-3}). Phosphorus levels were also very low. Therefore, the 10.24-ha soil fertility can be considered low. In general, soil properties did not differ between environments, although there were exceptions (Table 1). One exception was soil texture. In bamboo plots, soil was predominantly clayey while in non-bamboo plots soil was sandy clay loam. In addition, bamboo plots had soils that were significantly richer in potassium and magnesium. Consequently, base saturation was higher in bamboo plots. Although pH and Al^{3+} were not different between environments, bamboo plots had lower potential acidity (i.e. H + Al) and aluminum saturation. These differences indicate soils chemically more fertile in bamboo-dominated plots.

3.2. Vegetation structure and dynamics

We sampled a total of 10,617 trees at the end of the last census, being 902 seedlings, 3185 saplings, and 6530 adults. The corresponding number of species was ~58, 206, and 201 species, resulting in 246 species (since many seedlings remained undetermined, total richness may be underestimated). There were significant differences between bamboo-dominated and bamboo-free plots, but results varied according to the parameter or size class considered. Although there was a general tendency of higher mortality and recruitment in bamboo-plots, mortality was significantly higher only for adults, while for recruitment the same was found only for seedlings and saplings (Table 2). Mortality was significantly higher ($p < 0.0001$) in bamboo plots for all adult dbh classes (4.8–9, 10–19, and 20–30-cm dbh), except trees >30-cm dbh ($n = 478$, $t = 0.515$; $df = 122$; $p = 0.606$). Species density was the only variable that was significantly different for all size classes, being significantly higher in non-bamboo plots (Table 2). Diameter distribution analysis revealed strong differences between environments ($\Delta AIC_c = 259.6$). Both environments had great concentration of small-sized individuals (<5 cm dbh), but in the bamboo plots this concentration was more pronounced (Fig. 1).The same result was found when saplings were analyzed separately ($\Delta AIC_c = 68.5$). But when we considered only adults (dbh > 4.8 cm), the inverse

Table 1
Mean values ± SD of the surface soil (0–20 cm) parameters for bamboo and non-bamboo plots. The effect of bamboo dominance was tested using a *t*-test applied to the estimated coefficient in the optimum regression model. Because of very shallow bedrocks, two surface soil samples were not available for non-bamboo plots. Legend: P = phosphorus; H + Al = potential acidity; SEB = sum of exchangeable bases; CEC = cation exchange capacity. All units are mmol dm^{-3}, except where noted.

Soil parameter	Bamboo ($n = 49$)	Non-bamboo ($n = 105$)	*t*-Value (df)
Chemical			
pH (H_2O)	4.01 ± 0.27	3.93 ± 0.26	–1.61 (145)ns
Organic matter (g dm^{-3})	42.01 ± 9.08	40.23 ± 8.95	–0.56 (146)ns
P (mg dm^{-3})	9.76 ± 5.06	9.63 ± 4.56	–0.23 (146)ns
Na^+	0.905 ± 0.383	0.835 ± 0.337	0.07 (144)ns
K^+	3.57 ± 1.42	2.65 ± 1.09	4.38 (152)***
Ca^{2+}	11.27 ± 9.31	10.10 ± 11.66	–1.00 (142)ns
Mg^{2+}	6.68 ± 3.08	5.45 ± 3.02	2.52 (144)*
Al^{3+}	17.47 ± 6.50	19.56 ± 6.20	1.44 (148)ns
H + Al	82.61 ± 18.84	89.03 ± 19.26	2.74 (148)**
SEB	22.42 ± 12.49	19.03 ± 14.42	1.38 (152)ns
CEC	105.03 ± 26.13	108.07 ± 25.42	0.96 (150)ns
Base saturation (%)	19.42 ± 7.37	15.77 ± 8.38	–2.44 (148)*
Al saturation (%)	49.41 ± 13.60	57.13 ± 16.35	2.50 (150)*
Physical			
Sand (%)	44.87 ± 8.33	53.97 ± 7.84	3.26 (143)***
Silt (%)	14.89 ± 4.42	13.66 ± 3.35	–1.24 (143)ns
Clay (%)	40.25 ± 6.68	32.37 ± 7.96	–3.06 (143)**

ns = Non-significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

Table 2
Mean values ± SD of the vegetation parameters for bamboo and non-bamboo plots at each size class considered. The effect of bamboo dominance was assessed based on the estimated intercept coefficient of the regression model, tested using a *t*-test. For saplings, the number of plots in parenthesis refers to the sampling effort for the annual mortality, recruitment, and damage rate analysis.

Size class	Bamboo	Non-bamboo	*t*-Value (df)
Seedlings	$n = 70$	$n = 71$	
Density (trees m^{-2})	11.0 ± 10.2	10.2 ± 10.8	–0.33 (138)ns
Species (plot^{-1})	3.09 ± 1.58	3.94 ± 1.93	3.58 (136)***
Mortality (trees^{-1} yr^{-1})	18.6 ± 13.3	15.7 ± 15.7	–0.15 (134)ns
Recruitment (m^{-2} yr^{-1})	1330.6 ± 1345.1	636.9 ± 658.0	3.97 (138)***
Saplings	$n = 16$ (13)	$n = 38$ (29)	
Density (trees ha^{-1})	5250 ± 1628	6171 ± 3095	1.66 (50)ns
Basal area (m^2 ha^{-1})	4.75 ± 2.77	5.91 ± 2.48	1.80 (50)ns
Species (plot^{-1})	24.9 ± 9.5	31.7 ± 13.7	2.04 (50)*
Mortality (trees^{-1} yr^{-1})	2.3 ± 5.0	1.8 ± 2.7	1.86 (37)ns
Recruitment (m^{-2} yr^{-1})	14.53 ± 7.65	4.5 ± 4.5	2.72 (38)**
Damage (trees^{-1} yr^{-1})	14.1 ± 12.9	4.8 ± 6.2	2.65 (38)*
Physical damage	13.2 ± 13.3	2.6 ± 5.5	2.04 (37)*
Adults	$n = 49$	$n = 107$	
Density (trees ha^{-1})	438 ± 286	1328 ± 384	10.2 (151)***
Basal area (m^2 ha^{-1})	9.10 ± 9.25	37.90 ± 16.53	8.07 (152)***
Species (plot^{-1})	9.8 ± 5.5	29.4 ± 8.5	3.31 (152)**
Mortality (trees^{-1} yr^{-1})	3.5 ± 5.2	1.2 ± 1.7	6.93 (150)***
Recruitment (m^{-2} yr^{-1})	0.36 ± 0.33	0.32 ± 0.29	1.81 (144)ns

ns = Non-significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

result was found ($\Delta AIC_c = 26.6$). This was probably caused by a lack of individuals between 9 and 14-cm dbh in bamboo-plots, leading to a sort of bimodal distribution.

Sapling monitoring revealed a total of 175 damaged individuals that were not damaged in the first census (mean damage rate = 7.6 ± 9.7%). If damages that resulted in sapling mortality are added, damage rate is 9.5%. Overall and physical-induced damages were different between environments, both being higher in bamboo plots (Table 2). Physical disturbances accounted for 72% of damages, but their causes were quite different between environments. In bamboo-plots, the fall of bamboo culms (68.6%) and trees (31.4%) were the sole causes. In bamboo-free plots, tree (39.3%) and branch fall (30.6%) were the main causes. Damage by palm leaves and fallen bromeliads were rare and restricted to non-bamboo plots. The main consequences of damages were individuals thrown, bent, or broken that together comprise 78.7% of all damages. During the first census, the presence of resprouts was found on the stem of 26.7% of saplings (mean number of resprouting saplings per plot was 15.0 ± 8.3). Saplings with three or more stem resprouts could be found in the study area (see Supplementary material for an example).

4. Discussion

4.1. Soil properties

In general, soil chemical properties in bamboo and non-bamboo plots were very similar in the PECB. Base and aluminum saturations were the main exceptions. The tendency of soil under bamboo-stands to be richer in nutrients was contrary to the results of other bamboo-dominated forests (Veblen, 1982; Jingyi et al., 2002). But since the clay fraction influences the concentration of exchangeable bases and aluminum saturation (Laurance et al., 1999), the higher soil fertility was probably driven by the more clayey texture of soils under bamboo plots. Thus, is *G. tagoara* able to change soil texture or does it occurs preferentially over more clayey soils inside the plot? Although there are records of species changing its physical environment (e.g. Vitousek et al., 1987), it is difficult that *G. tagoara* is enhancing clay genesis or preventing clay translocation, simply because both processes take too long. In contrast, the inspection of the 10.24-ha soil map revealed that bamboo distribution matched quite well the distribution of a more clayey Cambisols (the occurrence of bamboo over rocky, shallow Leptosols was negligible). Therefore, it is more likely that the difference found in soil texture is due to the higher occurrence of bamboos in more clayey soils. Nevertheless, it is premature to affirm that *G. tagoara* overabundance has no effect over soil, since main processes such as nutrient cycling (e.g. nitrogen and carbon), leaching, uplifting, and soil water dynamics were not assessed here and may be affected by bamboo litter production and entangled root system (Veblen, 1982; Christanty et al., 1996).

As suggested by Griscom and Ashton (2006), there was little evidence that differences in vegetation structure and dynamics in bamboo plots are promoted by differences in soil. On the other hand, the morphopedological study of the 10.24-ha plot revealed that the clayey Cambisols that enclose the larger part of the bamboo-dominated plots suffer from frequent and intense creeping and planar landslides (Rodrigues, 2005). Actually, there is evidence that this difference in clay fraction inside the 10.24-ha plot is the result of an old landslide. Besides the higher clay fraction in upper horizons, the limits of different Cambisol subtypes in the plot are coincident to sudden changes in slope angle. Thus, the origin of bamboo-dominated areas in the studied site may be related to natural disturbances instead of human-induced ones.

4.2. Vegetation structure and dynamics

The general pattern found for other *Guadua*-dominated forests (Griscom and Ashton, 2003; Silveira, 2005; Nelson et al., 2006; Fantini and Guries, 2007) was confirmed here: *Guadua*-dominated areas have lower density and basal area of trees >5-cm dbh (for seedlings and saplings, differences are not significant). This pattern is the result of higher recruitment in the seedling and sapling stages that is offset by higher adult mortality, which is three fold bigger than in non-bamboo plots. Therefore, reduced density in these forests are the result of higher mortality rather than the lower recruitment suggested by Griscom and Ashton (2006). In other words, bamboo-dominated plots are more dynamic: there is more tree species germination and growth, but there is more mortality as well.

Sapling monitoring revealed that bamboo-dominated plots had more physical damages (mainly caused by bamboo culms) and a higher frequency of resprouting individuals. The smaller number of trees between 10 and 15-cm dbh in bamboo plots may indicate a critical tree size for bamboo-induced damages (*G. tagoara* loads exist up to 20 m high). These results agree with Griscom and Ashton (2006) findings and partially support their bamboo crushing hypothesis formulated for other *Guadua*-dominated forests. However, both studies only monitored damages in small trees (<5-cm dbh) and neither quantified the chance of death following damage that is often negligible for trees >10-cm dbh (Clark and Clark, 1991). In addition, both studies found that the mortality of small trees was only marginally higher in bamboo plots. So although *Guadua* loading is an intuitive explanation for higher adult mortality in bamboo-dominated areas, there is little direct evidence to support it. Therefore, we cannot disregard that adult trees are more exposed to wind-throw (Okutomi et al., 1996), severe drought effects, or other types of disturbances/stresses. The existence of different tree damage levels between bamboo and non-bamboo stands reported by Griscom and Ashton (2006) does not guarantee that damages are directly related to bamboo load or that bamboo crushing is not triggered by other types of disturbances. And if sapling mortality is filtering species able to resprout at the expense of others, then physical damage could be even less important in explaining the higher mortality of adults in areas with bamboo.

The lower species density found in bamboo plots was similar to other bamboo-dominated forests (Veblen, 1982; Taylor and Zisheng, 1988; but see Young, 1991), and it is probably a combination of pre and post-germination processes. Bamboo plots are more seed limited (Rother et al., 2009) meaning that many sites receive less or no seeds of certain species. However, the same authors found that the overall seed rain in bamboo plots is more species-rich. Therefore, it seems that the main process reducing seedling richness act after seed germination, and is probably related to the physical or physiological stress of bamboo-dominated areas. The ability to respond positively to damages varies among species (Clark and Clark, 1991; Simões and Marques, 2007; Lasso et al., 2009) and many can have its performance compromised due to an excess of light/heat or to a lack of soil water availability (Takahashi and Murata, 2008). In addition, it is expected that differences in species richness should be accompanied by differences in composition (Silveira, 2005). In bamboo-dominated areas plausible larger contributions of light-wood pioneer species may well influence community growth and survival, being an extra factor that could explain the differences found between environments. If we assume that non-pioneers suffer more intensively from bamboo competition, then a general lack of opportunities for these species may also contribute to decrease tree species richness.

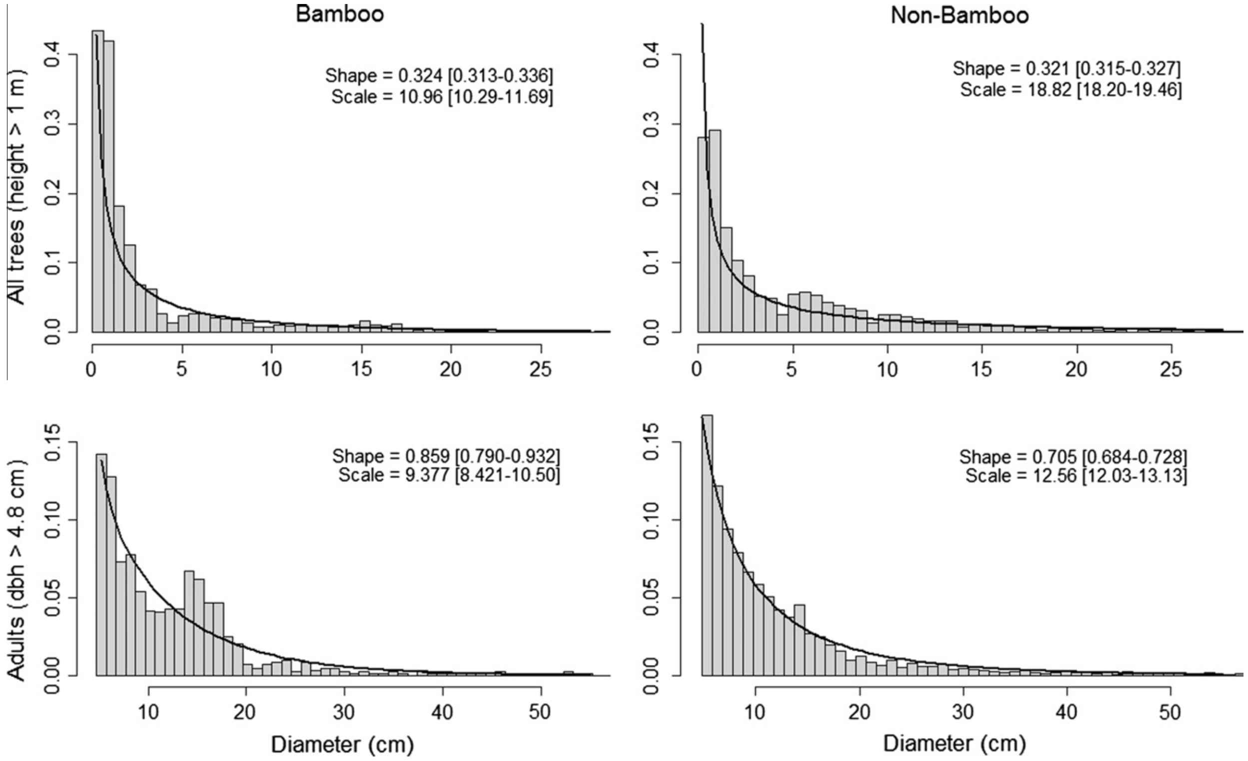

Fig. 1. Comparison of the tree diameter distribution between bamboo and non-bamboo plots. On top, the comparison including saplings and adults (all individuals taller than 1 m). Below, the comparison of adults (individuals with dbh $\geqslant$ 4.8 cm). Shape and scale are the maximum likelihood estimates of the Gamma distribution fit (black bold line), presented along with their 95% confidence intervals in brackets.

4.3. Origin, maintenance and implications of bamboo overabundance

The underlying processes presented in *G. tagoara*-dominated forests are very similar to Amazonian *Guadua* forests, suggesting that a high expansion potential is widespread in *Guadua*. The long periods until seed production, which should lessen bamboo potential as an "invader" (Rejmánek and Richardson, 1996), seems to be overwhelmed by an opportunistic and aggressive rhizomatous growth (Alves, 2007). But if *G. tagoara* is similar to Amazonian *Guadua*, why bamboo-dominated areas in the Amazon are orders of magnitude larger than in the Atlantic Forest (10^2–10^4 vs. 10^{-1}–10^0 km^2, respectively – Nelson et al., 2006; Araujo, 2008)? Time since the expansion processes began seems to be a weak explanation because the Atlantic Forest devastation began centuries earlier. More likely, since bamboo needs increases in light (Burman and Filgueiras, 1993; Judziewicz et al., 1999), the answer to this question may lay in the characteristics of the disturbance agents causing such light increases. Fire and forest conversion are widespread and severe vectors of bamboo expansion in the Amazon (Silveira, 2005), but are less common in the protected Atlantic Forest remnants. In the Atlantic Forest, illegal palm-heart harvesting are more common but generally less intense vectors of bamboo expansion (Fantini and Guries, 2007). Here we proposed that severe and sporadic landslides may be important in steep areas, as well as man-induced disturbances as proposed by Araujo (2008). Altogether, these differences in the pattern of disturbance may have caused a slower and patchy-fashion expansion of *Guadua*-dominated Atlantic Forests.

Once *Guadua* successfully colonize a new clearing, some mechanisms are needed to maintain the occupation. Other researchers have efficiently shown how semi-scandent *Guadua* clumps can work as structural parasites, preventing normal forest regeneration (Silveira, 1999; Griscom and Ashton, 2006). Other disturbances (e.g. wind and soil movements) may also be important (Okutomi et al., 1996). But after mast flowering and bamboo dieback, other mechanisms must take place to avoid competition with tree species. In the permanent plot, *G. tagoara* synchronously flowered and died during 2005 and 2006, and bamboo seedlings from the mast fruiting efficiently established in the same opened areas. A similar observation was made by Araujo (2008) in a nearby forest. The numerous seedling bank (see Supplementary material) and their rapid growth (height growth up to 4 m yr^{-1} – R.A.F. Lima unp. data) may be an efficient strategy to gain competitive advantage over trees and to recover space after bamboo die-off.

Therefore, besides massive seed production and rapid growth, we hypothesize that the absence of large, generalist herbivores may be favoring *Guadua* expansion (*sensu* Parker et al., 2006). Large mammals (e.g. tapirs, agoutis, peccaries, and deer) are major herbivores (Asquith et al., 1997; Silman et al., 2003) and they often prey on bamboo seeds, seedlings, and young shoots (Taylor and Zisheng, 1987; Silveira, 1999, 2005; Franklin, 2005). If these herbivores are not present, the great abundance of bamboo seeds and seedlings is not offset by a higher consumption by herbivores. Therefore, hunting of large mammals (a common feature even inside Atlantic Forest protected areas – Galetti et al., 2009) may indirectly favor *Guadua* expansion, a possible example of expansion through enemy release. And since illegal palm-heart harvesting generally takes place coupled with hunting, both illegal activities may work synergistically to create ideal environments for bamboo expansion. Thus, we predict that defaunated areas are more prone to *Guadua* expansion. It is important to stress that the absence of large herbivores may not be the only cause of bamboo overabundance, but this and other human-induced causes may be more directly related to the recent *Guadua* expansion in the study region.

Consequences of *G. tagoara* overabundance to conservation are hard to predict, especially because we still need monitoring in other areas to assess *G. tagoara* expansion rate in the entire Atlantic Forest (Araujo, 2008). If it is expanding fast and everywhere, then the local effects seen here will soon become a major and regional threat. The structure and dynamics of the Atlantic Forest remnants could be drastically altered, changing the community composition and enhancing the chance of biological invasions (Simberloff and von Holle, 1999). It probably will not cause regional extinctions (Gurevitch and Padilla, 2004; Sax et al., 2007), but forest species certainly will be displaced (Mack et al., 2000), including animals (e.g. Touyama et al., 1998). Bamboo masting events could also increase the dissemination of wildfires (Keeley and Bond, 1999; Veldman and Putz, 2011), emerging diseases (e.g. Hantavirus – Jaksic and Lima, 2003) and the invasion of exotic species (e.g. *Musa ornata*). However, if *G. tagoara*-dominated areas are only expanding in the studied region, then more detailed studies are needed to assess local expansion causes and if this is a cyclical expansion processes. It is also important to assess the effects of *G. tagoara* overabundance in other important variables (e.g. beta diversity), other organisms (e.g. animals), and other areas (e.g. economic potential of *G. tagoara* for smallholders). Until then any attempt to control this bamboo species remains premature.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2012.01.015.

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